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REGULATION OF ELECTRON TRANSPORT IN PHOTOSYSTEM-II FRAGMENTS BY MAGNESIUM IONS *

YASUSI YAMAMOTO and BACON KE

Charles F. Kettering Research Laboratory, Yellow Springs, OH 45387 (U.S.A.)

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Summary

In Photosystem-II reaction-center particles (TSF-IIa) fractionated from spinach chloroplasts by Triton X-100 treatment, divalent cations appear to regulate electron-transport reactions. Oxidation of cytochrome *b*-559 after illumination of the particles was accelerated by the presence of Mg^{2+}, whereas photoreduction of 2,6-dichlorophenolindophenol (DCIP) by diphenyl carbazide was inhibited, both at a half-effective concentration of Mg^{2+} of approx. 0.1 mM.

The site of regulation was shown to be on the oxidizing side of Photosystem II, near *P*-680, based on the effects of actinic-light intensity and nature of the electron donors on DCIP photoreduction. Mg^{2+} was effective in quenching chlorophyll fluorescence in TSF-IIa particles, but the quenching was sensitive to the presence of 3(3,4-dichlorophenyl)-1,1-dimethylurea. In the reaction-center (core) complex of Photosystem II, where the light-harvesting chlorophyll-protein complex is absent, there seems to be no regulation by Mg^{2+} on excitation-energy distribution.

Introduction

Cations can regulate the distribution of excitation energy between the two photosystems in chloroplasts. The degree of regulation depends on the species, valency and concentration of the ions. At low concentrations, Mg^{2+} was shown

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Abbreviations: TSF-II (TSF-IIa), Triton-fractionated Photosystem-II subchloroplast fragments (subfragments produced by further fractionation of TSF-II); DCIP, 2,6-dichlorophenolindophenol; DCMU, 3(3,4-dichlorophenyl)-1,1-dimethylurea; Q, primary electron acceptor of Photosystem II; Chl, chlorophyll; Cyt, cytochrome.

to inhibit energy transfer from Photosystem II to Photosystem I, as inferred from its effects on chlorophyll fluorescence yield [1—3]. Monovalent cations seem to induce energy transfer between the two photosystems, thus working opposite to Mg^{2+} [4]. In addition, there are also non-specific electrical interactions between ions and charged thylakoid-membrane surfaces, which can result in the regulation of primary photosynthetic reactions [5—9].

The site of cation action in chloroplasts has been one of the major concerns in terms of regulation of distribution of excitation energy among the two photosystems. The development of energy-transfer capacity in etioplasts during greening was related to thylakoid stacking after exposure of the etioplasts to continuous light [10,11]. A light-harvesting pigment-protein complex was shown to play a significant role in this stacking process [12]. Furthermore, grana stacking was demonstrated by the addition of cations to salt-depleted agranal chloroplasts [13—15]. It was also reported that the Mg^{2+}-induced inhibition of energy transfer was eliminated by an antibody preparation against the light-harvesting pigment-protein complex [16]. These results suggest that (a) cations bind to the light-harvesting pigment-protein complex and regulate energy transfer between the two photosystems, and (b) the light-harvesting complex is necessary for the formation of grana stacks, a process which seems to be regulated by cations also.

Recently, some authors suggested specific effects of divalent cations on the Photosystem-II reaction center using photosystem-II subchloroplast particles [20—23]. Wydrzynski et al. [20] showed that Mg^{2+} induced an increase in the fluorescence ratio F_{695nm}/F_{685nm} in Photosystem II particles. Since F695 emission has been suggested to arise from Photosystem-II reaction centers, their results demonstrated a direct effect of Mg^{2+} on Photosystem-II reaction centers. Davis et al. [21] showed regulation of energy transfer in Photosystem-II particles by divalent cations. The mode of regulation was shown to be dependent on whether the particle contains a light-harvesting complex or not [21]. Regulation of excitation-energy transfer in Photosystem-II particles in the presence of Mg^{2+} was also suggested by Horton and Croze [22].

In the present study, we examined the effects of Mg^{2+} on oxido-reduction of Cyt *b*-559, DCIP photoreduction and chlorophyll fluorescence changes in TSF-IIa particles. Our results suggest that there exists a regulation on electron transport, but not on excitation-energy transfer in the presence of Mg^{2+}. We also showed a possible site of regulation by Mg^{2+} on electron transport in Photosystem-II particles.

Materials and Methods

TSF-IIa particles were prepared according to Ref. 24. The particles have 1 Cyt *b*-559 per 34 chlorophyll molecules, no detectable *P*-700, and a DCIP-reduction activity (in fresh preparatons) of approx. 1000 μmol/mg Chl per h.

Light-induced absorbance changes associated with photoreduction of Cyt *b*-559 and DCIP were measured with a dual-wavelength spectrophotometer [24]. The measuring and the reference wavelengths were, respectively, 430 and 570 nm for Cyt *b*-559 and 570 and 500 nm for DCIP reduction. In the measurements of Cyt *b*-559 absorbance changes, illumination was limited to

3 s by means of an electronic shutter to avoid interference by absorption changes due to irreversible photobleaching of chlorophyll at 430 nm. As the initial rate of DCIP photoreduction in TSF-IIa is dependent on preillumination history of the preparation, we always used completely dark adapted preparation for each measurement. Saturating red actinic light was provided by a tungsten-light source using a Corning 2-58 filter (transmitting wavelengths longer than 630 nm) and 2 inches of $CuSO_4$ solution (total incident energy; $5 \cdot 10^5$ ergs/cm^2 per s). If necessary, the intensity of actinic light was varied and the total intensity remeasured by a Kettering-Yellow Springs Instrument radiometer. An EMI 9558 photomultiplier tube shielded by two Corning 4-96 filters was used for signal detection. Temperature of the reaction mixture was usually adjusted to 21°C by flowing thermostated water through an insulated cuvette jacket (Cary model 1444100).

Slow fluorescence changes of chlorophyll at room temperature were measured by a double-beam fluorometer (Cary accessary model 56-231). Fluorescence was excited by blue light (intensity, 500—1000 ergs/cm^2 per s) from a tungsten-halogen lamp with two Corning 4-96 filters and two Corning 1-69 heat-absorbing filters. Fluorescence passed through a monochromator (wavelength setting 685 nm, bandwidth, 8 nm) and two Corning 2-58 filters was detected by a Hamamatsu R-928 photomultiplier tube and, after processing, the signal was recorded on an XY-recorder.

Fast fluorescence induction in TSF-IIa particles was also excited by blue light and detected by an EMI 9558 photomultiplier tube shielded by two Corning 2-58 filters and one Corion interference filter (peak wavelength, 685 nm). The emission signal amplified by a Tektronics 1A5 current amplifier was first recorded by a Biomation-805 transient recorder and then fed to a Fabritec signal averager and finally transcribed on an XY-recorder. Excitation of the sample and recording of the signal by the Biomation-805 recorder were initiated by the opening of a Uniblitz electronic shutter.

The standard reaction mixture contained TSF-IIa particles equivalent to 15 μg Chl/ml in 0.02 M sodium phosphate buffer, pH 7.0, in a final volume of 2.0 ml. When measuring DCIP photoreduction, 30 μM DCIP and electron donors of various concentrations were added. Salts of monovalent- and divalent-cations were used at concentrations indicated in the figure legends.

Results

Effects of Mg^{2+} on Cyt b-559 oxido-reduction in TSF-IIa particles

The Cyt *b*-559 in TSF-IIa particles is present in the low-potential form, with $E_{m,7}$ of about 60 mV [25]. In isolated subchloroplasts, Cyt *b*-559 is present in the oxidized form. It is readily photoreduced, followed by a slow reversal to the oxidized form in the dark (Fig. 1). The kinetics of dark oxidation of Cyt *b*-559 was apparently first order and the addition of Mg^{2+} induced a significant increase in the rate of re-oxidation. The $MgCl_2$ concentration required to accelerate cytochrome re-oxidation to the half-maximum value was about 0.1 mM, and the Mg^{2+}-effect was saturated at 0.5 mM (Fig. 2). Salts of monovalent cations such as KCl was also effective in accelerating the dark oxidation of Cyt *b*-559, but a much higher concentration of the salt was required to bring about

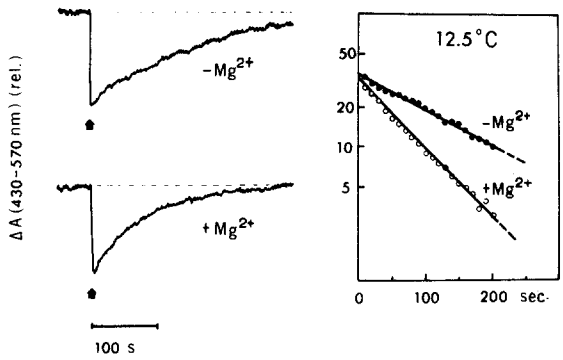


Fig. 1. Time course of light-induced reduction of Cyt *b*-559 and its dark oxidation in TSF-IIa particles in the presence and absence of $MgCl_2$. No electron donor was added. Arrow indicates a 3-s illumination.

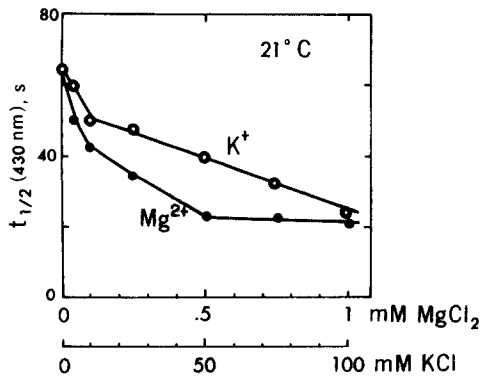
the same effect as divalent cations (Fig. 2).

Effects of other divalent cations on Cyt *b*-559 oxidation were examined. Ca^{2+} was as effective as Mg^{2+} in significantly accelerating the dark oxidation of Cyt *b*-559, but Mn^{2+} had no effect on cytochrome oxidation (data not shown); effects of $MgCl_2$ or $CaCl_2$ seem to be rather specific.

$MgCl_2$, however, had only a slight effect on the initial rate of photoreduction of Cyt *b*-559. About 10% decrease was observed in the rate of Cyt *b*-559 reduction by the addition of 0.1 mM $MgCl_2$, and the effect became saturated at this concentration.

Effects of Mg^{2+} on DCIP-photoreduction in TSF-IIa particles

TSF-IIa showed a high DCIP-photoreduction activity when diphenyl carbazide was used as an electron donor. The initial rate of DCIP reduction was decreased by the addition of $MgCl_2$. The concentration of $MgCl_2$ for half inhibi-



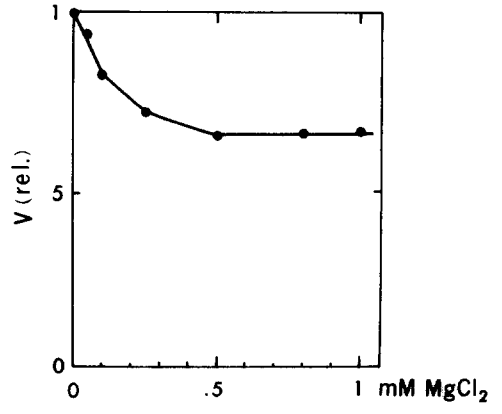


Fig. 2. Effect of $MgCl_2$ and KCl on the half-time of Cyt *b*-559 oxidation after illumination of TSF-IIa particles. No electron donor was added.

Fig. 3. The initial rate of DCIP photoreduction in the presence of varying amounts of $MgCl_2$. 0.1 mM of diphenyl carbazide was added as the electron donor.

tion was also 0.1 mM (Fig. 3), which was exactly the same as that required to accelerate Cyt *b*-559 re-oxidation. These results suggested that both Cyt *b*-559 re-oxidation and DCIP reduction was regulated at the same site on the membrane by Mg^{2+}.

Effects of $MgCl_2$ on DCIP-photoreduction was also examined using other electron donors (Table I). Optimum reagent concentrations were chosen for producing maximum DCIP-reduction activity. Even when other electron donors were used, Mg^{2+} induced an inhibition in DCIP reduction, with $MnCl_2$ being the only exception. Babcock and Sauer have presented evidence from EPR study of chloroplast that a hydrophilic electron donor such as Mn^{2+} feeds electrons directly to $P\text{-}680^+$ and lipophilic donors such as diphenyl carbazide or phenylenediamine donate to Z^+, the oxidized secondary electron donor of Photosystem II [26]. Our results also show that in TSF-IIa particles, Mn^{2+} can donate electrons to a site different from that for other reagents, irrespective of their hydrophobicity. Because the extent of inhibition of DCIP reduction by Mg^{2+} is dependent on the type of electron donor used, it is supposed that the Mg^{2+} inhibition site is located on the oxidizing side of Photosystem II, but near *P*-680.

The Mg^{2+}-induced effect on DCIP reduction with diphenyl carbazide as an electron donor was compensated by further addition of diphenyl carbazide (100 μM), but not by addition of more DCIP (up to 30 μM). This also suggests that the rate-limiting step in Mg^{2+}-inhibited DCIP reduction is on the oxidizing side of Photosystem II (Table II).

Effects of actinic-light intensity on DCIP and Cyt b-559 photoreduction

To examine the possibility that there is a control of excitation-energy distribution by Mg^{2+} in TSF-IIa particles, we varied the intensity of actinic light and measured the initial rate of DCIP-photoreduction in the presence and absence of $MgCl_2$ (Table III). The extent of inhibition of DCIP-photoreduction by Mg^{2+} was almost constant (approx. 20%) under illumination at various light intensities. Data plotted in a double-reciprocal form according to the formulation of Lumry and Spikes [27,28] yielded straight lines (Fig. 4):

$$\frac{1}{v} = \frac{1}{K_D} + \frac{1}{K_L} \cdot \frac{1}{I}$$

In this formulation, v is the reaction rate, I the light intensity, K_D the rate constant of the rate-limiting step in electron transport under infinite light intensity, and K_L the efficiency of light reaction, respectively. As seen in Fig. 4a, when $MgCl_2$ was present in the reaction mixture, the intercept to the ordinate (K_D) was shifted without change in the line slope. If there is a control of excitation-energy distribution by Mg^{2+} in the TSF-IIa particle, some change in the efficiency of photoreaction, thus the line slope, should occur as the light intensity varies. The observed effects of Mg^{2+} on DCIP photoreduction are probably not to be ascribed to a regulation of excitation-energy distribution in these particles by Mg^{2+}, but to an inhibition of electron transport.

We also studied the relationship between the actinic-light intensity and the initial rate of photoreduction of DCIP and Cyt *b*-559 in the presence and

TABLE I

EFFECTS OF Mg^{2+} ON DCIP PHOTOREDUCTION WITH DIFFERENT ELECTRON DONORS

The reaction mixture (2.0 ml) contained TSF-IIa particles at 7.5 μg Chl/ml, 15 μM DCIP, and indicated amount of electron donor in potassium phosphate buffer (0.02 M, pH 7.0). Temperature. 20°C.

Electron donors	DCIP reduction (μmol/mg Chl/h)		% Inhibition
	$-MgCl_2$	$+MgCl_2$ (0.5 mM)	
Diphenyl carbazide (0.1 mM)	210	157	25
Hydroquinone (0.01 mM)	149	123	17
NH_2OH (2 mM)	168	123	27
$MnCl_2$ (0.1 mM)	117	115	2

absence of DCMU. Satoh et al. [29] showed that electron-transport inhibitors of Photosystem II affect either K_D or K_L in the Lumry-Spikes plot, depending on whether the reagent acts on the oxidizing or reducing side of Photosystem II [29]. As shown in Fig. 4b, in TSF-IIa particles, DCMU inhibited DCIP photoreduction with diphenyl carbazide as an electron donor, and the Lumry-Spikes plot showed a change only in K_L. Thus the two straight lines had the same intercept on the ordinate but with different slopes. That was also the case when Cyt *b*-559 photoreduction was inhibited by DCMU (Fig. 4c). Thus, the inhibition pattern of electron transport by Mg^{2+} in the Lumry-Spikes plot showed a marked contrast when DCMU is present. Since the site of DCMU inhibition is known to be on the reducing side of Photosystem II, between Q and plastoquinone, these results again show the site of inhibition by Mg^{2+} to be located on the oxidizing side of Photosystem II.

Quenching of chlorophyll fluorescence by Mg^{2+}

Chlorophyll fluorescence of TSF-IIa particles was quenched when $MgCl_2$ (5 mM) was added to the reaction mixture under illumination (Fig. 5). KCl at the same concentration had no effect on the fluorescence. To observe strong quenching of fluorescence by the addition of Mg^{2+}, a higher concentration of

TABLE II

DEPENDENCE OF DCIP-PHOTOREDUCTION ACTIVITY ON SUBSTRATE CONCENTRATION IN THE PRESENCE AND ABSENCE OF Mg^{2+} (20°C)

Control reaction mixtures: in (A) TSF-IIa particles at 15 μg Chl/ml, 15 μM DCIP, and 50 μM diphenyl carbazide (DPC) in 0.02 M, pH 7.0, sodium phosphate buffer; in (B) same as in (A) except 100 μM DPC.

Conditions		% Activity
A	Control	100
	Control + $MgCl_2$ (0.5 mM)	73
	Control + $MgCl_2$ (0.5 mM) + DCIP (15 μM)	77
	Control + $MgCl_2$ (0.5 mM) + DPC (50 μM)	100
	Control + DPC (50 μM)	108
B	Control	100
	Control + DCIP (15 μM)	100

TABLE III

EFFECT OF Mg^{2+} ON DCIP-PHOTOREDUCTION ACTIVITY AT DIFFERENT ACTINIC INTENSITIES

Light intensity (ergs/cm^2/s)	Relative activity		% Inhibition
	$-Mg^{2+}$	$+Mg^{2+}$ *	
7.0×10^5	12.5	10.0	20
1.4×10^5	7.5	6.0	20
1.0×10^5	3.3	2.5	22
5.0×10^4	3.5	2.7	23

* $MgCl_2$: 0.5 mM; 20° C.

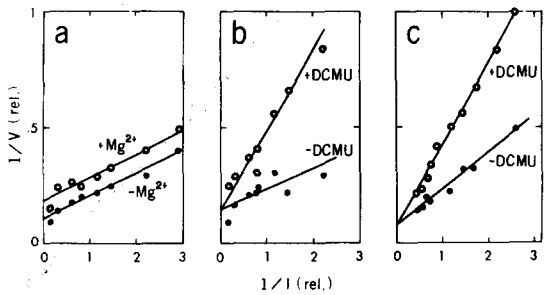


Fig. 4. The Lumry-Spikes plot for DCIP photoreduction in the presence of $MgCl_2$ (a), DCMU (b), and that for Cyt *b*-559 photoreduction in the presence of DCMU (c). One unit for the reciprocal light intensity corresponds to 10^5 ergs/cm^2 per s. For DCIP photoreduction, 50 μM of diphenyl carbazide was added as the electron donor. Other reagents were: $MgCl_2$, 0.5 mM; DCMU, 1 μM in (b) and 3.3 μM in (c).

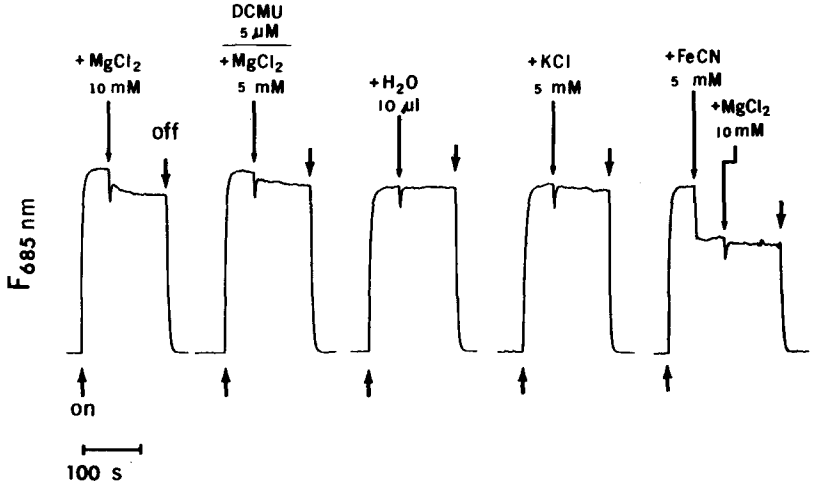


Fig. 5. $MgCl_2$-induced quenching of chlorophyll fluorescence (measured at 685 nm) in TSF-IIa particles. Instrument time constant was 2.5 s. A TSF-IIa preparation was used at a concentration of 7.5 μg Chl/ml. After addition of reagents to the illuminated cuvette, the reaction mixture was stirred momentarily. Mixing artefacts were checked by adding the same amount of distilled water.

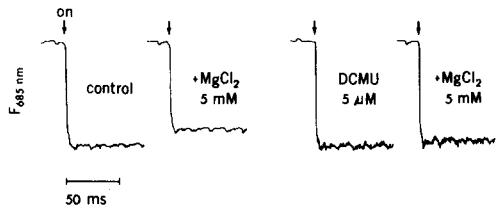


Fig. 6. Effect of $MgCl_2$ on the F_0 level (downward trace represents fluorescence increase) of chlorophyll fluorescence in TSF-IIa particles. Rate of fluorescence increase was limited by the effective opening time of the electronic shutter (approx. 0.5 ms). Instrument time constant was 3 μs. Measurements were carried out either without (left) or with (right) 5 μM of DCMU.

$MgCl_2$ than that needed for other reactions (approx. 0.5 mM) was required, partly due to a low actinic intensity that limits reduction of Q (see Discussion). The Mg^{2+}-induced quenching was sensitive to DCMU-inhibition; smaller quenching was observed in the presence of 5 μM DCMU. Thus, effects of Mg^{2+} on chlorophyll fluorescence seem to be dependent on Q. These results are at variance with those observed by Horton and Croze with their Photosystem-II particles [22].

$MgCl_2$ had a slight effect on the F_0 level of chlorophyll fluorescence, suggesting direct effects of Mg^{2+} on the reaction-center complex of Photosystem II (Fig. 6).

Accerelated oxidation of Q by the addition of Mg^{2+} was also confirmed by determining the ratio of concentration of oxidized form of Q to that of total Q from fluorescence induction curves according to the formulation of Malkin and Kok [30] (our data not shown). Mg^{2+}-induced quenching of chlorophyll fluorescence seems to be due to an acceleration of oxidation of Q by secondary electron acceptors. Furthermore, the fluorescence-rise curve does not show a sigmoid shape, suggesting an absence of energy transfer among Photosystem-II units [31,32].

Discussion

The evidence that Mg^{2+} inhibited DCIP photoreduction (supported by artificial electron donors) and accelerated Cyt *b*-559 re-oxidation at the same time (concentration for half effect was 0.1 mM) indicates the existence of a cation-sensitive regulatory site on the common electron-transport pathway of both reactions. Mg^{2+} also accelerated the re-oxidation of Q judging from chlorophyll-fluorescence measurements. The Lumry-Spikes plot for DCIP photoreduction and Cyt *b*-559 photoreduction in the presence of $MgCl_2$ and DCMU suggest that the inhibition site of Mg^{2+} is located on the oxidizing side of Photosystem II. The Mg^{2+}-inhibition of DCIP photoreduction with diphenyl carbazide as an electron donor was compensated by the addition of a higher concentration of diphenyl carbazide, but not by addition of the electron acceptor DCIP. Furthermore, the inhibition of DCIP reduction was dependent on the nature of the electron donor used. These results again suggest that the site of Mg^{2+} action is located on the oxidizing side of Photosystem II, and close to *P*-680. In the fluorescence-quenching measurements, a higher concentration of Mg^{2+} than

that needed for other reactions was required. One interpretation is that the site of Mg^{2+} action is close to *P*-680, and the effect of Mg^{2+} on Q is rather indirect.

Another important evidence suggesting a regulation site in TSF-IIa particles was obtained by examining the temperature-induced effects on Cyt *b*-559 oxido-reduction in TSF-IIa particles [33]. Oxidation of Cyt *b*-559 after illumination was highly sensitive to temperature and the Arrhenius plot of the decay half-time showed an apparent discontinuity at 16—18°C. A similar but less distinct break point was also observed in the Arrhenius plot for the initial rates of Cyt *b*-559 photoreduction. The discontinuity in the Arrhenius plot was eliminated by the addition of 0.5 M $MgCl_2$, an amount also needed to accelerate the dark oxidation of Cyt *b*-559. The effect of Mg^{2+} on the phase change could be a reflection of cation-induced control of microenvironment, resulting in the regulation of electron transport in TSF-IIa particles.

One possible candidate for the cation-regulation site is a chlorophyll molecule or a chlorophyll-protein complex near the Photosystem-II reaction center in TSF-IIa particles. Malkin and Bearden [34] and Visser et al. [35,36] (also Ref. 24) suggested a chlorophyll molecule near the reaction center to be a possible electron donor to *P*-680 by studying EPR properties of chlorophyll at low temperature. Our present results also support the idea that chlorophyll is an intermediate electron carrier between *P*-680 and Cyt *b*-559; photobleaching of bulk chlorophylls monitored at 422 nm was diminished in initial rate by 27% in the presence of 0.5 mM $MgCl_2$, the same concentration as that which induces an acceleration of Cyt *b*-559 oxidation. In addition, photobleaching of chlorophyll caused by longer, steady illumination of TSF-IIa was shown to be eliminated when diphenyl carbazide was added as an electron donor. In TSF-IIa particles, the turn-over rate of Cyt *b*-559 was very slow and charge separation of Photosystem-II reaction center, as monitored by absorbance change of *C*-550, occurred irrespective of Cyt *b*-559 change [37]. In chloroplasts, Cyt *b*-559 may be photooxidized at —197°C, but chemical oxidation prior to freezing does not limit the photoreduction of *C*-550 at —197°C [37,38]. Thus, it is probable that electron donors other than Cyt *b*-559 are capable of reducing $P\text{-}680^+$.

We suppose here that (a) chlorophyll molecules may function as an intermediate electron carrier between *P*-680 and Cyt *b*-559 and (b) the microenvironment of the chlorophyll molecules may be changed by the addition of divalent cations, resulting in regulation of electron transport in TSF-IIa particles. Fig. 7 shows an electron-transport scheme for Photosystem II involving the regulation site by Mg^{2+}.

Although the physiological significance of Mg^{2+}-induced effects in Photosystem-II reaction centers is not readily obvious from the study using Photosystem-II particles, we can deduce some possible roles of Mg^{2+} in the in vivo reactions from our results. When chloroplasts are illuminated and H^+ is actively pumped up into the thylakoid, Mg^{2+} bound to the inner surface of the membrane may be released into the inner thylakoid space by ion exchange as previously suggested by Barber et al. [17—19]. Release of Mg^{2+} facilitates the transfer of absorbed excitation energy from Photosystem II to Photosystem I, which results in an increase in efficiency of non-cyclic electron transport via Photosystems I and II. On the other hand, binding of Mg^{2+} to the light-harvest-

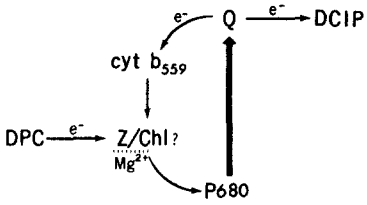


Fig. 7. A model for a possible site of electron-transport regulation by Mg^{2+} in TSF-IIa particles.

ing chlorophyll-protein complex in thylakoid membrane brings about inhibition of energy transfer from Photosystem II to Photosystem I, and there occurs an increase in quantum yield of the Photosystem-II reaction [1—3]. Mg^{2+} bound to the oxidizing side of Photosystem II may activate cyclic electron transport around Photosystem II, probably through Cyt *b*-559, and at the same time inhibits oxidation of H_2O so as to diminish supply of excess electrons in the Photosystem-II electron-transport system.

In summary, results presented in this work and in the accompanying paper [39] show that in the reaction-center (core) complex of Photosystem II (TSF-IIa), where the light-harvesting chlorophyll-protein complex is absent, there is regulation by Mg^{2+} on electron transport but a less likelihood on the distribution of excitation energy.

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